RED-COCKADED WOODPECKERS VS RAT SNAKES: THE EFFECTIVENESS OF THE RESIN BARRIER

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ABSTRACT.—Red-cockaded Woodpeckers (*Picoides borealis*) excavate resin wells in the immediate vicinity of roost and nest cavity entrances. Resin wells are worked regularly, resulting in a copious and persistent resin flow that coats the tree trunk, especially below cavity entrances. Red-cockaded Woodpeckers also scale loose bark from cavity trees and closely adjacent trees. These two behaviors result in smooth, sticky surfaces surrounding cavity entrances. Climbing experiments on cavity, scaled, and control trees using rat snakes (*Elaphe obsoleta*) demonstrate that these behaviors produce a resinous barrier that is highly effective in preventing predatory snakes from gaining access to active Red-cockaded Woodpecker cavities. *Received 23 Jan. 1989, accepted 15 May 1989.*

Red-cockaded Woodpeckers (*Picoides borealis*) and rat snakes (*Elaphe obsoleta*) are sympatric over an extensive area in the southeastern United States (Jackson 1971, Conant 1985). Unique aspects of the behavioral biology of the Red-cockaded Woodpecker have been hypothesized as adaptations to reduce predation by rat snakes (Dennis 1971a, Ligon 1970). In this paper, we report experimental data supporting the hypothesis that cavity protection behavior, specifically when this behavior results in copious fresh resin accumulation adjacent to cavity entrances, significantly reduces the ability of rat snakes to climb Red-cockaded Woodpecker cavity trees.

The Red-cockaded Woodpecker primarily inhabits mature pine forests over much of the southeastern United States (Jackson 1971) where habitat alteration due to various management procedures has resulted in the species being placed on the Federal list of endangered species (Thompson and Baker 1971, Wood 1983).

Southeastern pine forests, due to climate and the historical importance of fire, provide few dead trees and limbs for cavity construction by woodpeckers (Ligon 1970, 1971). The Red-cockaded Woodpecker, unlike most other woodpecker species, uses living pines as cavity sites, with rare exceptions (Ligon 1970, Patterson and Robertson 1983, Wayne 1910). The selection of living pines, which produce copious resin flows when mechanical damage occurs, places constraints on cavity location and architecture. Cavities need to be located in trunk segments of sufficient diameter

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and age to insure that the occupied chamber is located in the nonliving central heartwood to avoid resin accumulation in the chamber (Beckett 1971; Dennis 1971a, b). Consequently, almost all cavities are located on the bole of the pine, usually below the lowest branches (Ligon 1970). Entrance tunnels, which necessarily pass through living, resin-transporting tissues to reach the nonliving heartwood, are sloped upward. Thus, resin flows are directed toward the exterior of the tree and away from the cavity chamber (Ligon 1970). The excavation of small ancillary holes, termed resin wells, is associated with cavity construction by Red-cockaded Wood-peckers (Ligon 1970, Dennis 1971a). Several resin wells typically are associated with each cavity; these generally are located within a meter above and below the cavity entrance. Resin wells are worked regularly by the birds so that copious resin flow persists (Dennis 1971a, Ligon 1970). An essentially complete coat of fresh resin eventually accumulates on the tree surface surrounding the cavity entrance, often extending several meters below the entrance. In addition, adjacent trees may also have a limited number of resin wells (Dennis 1971a, D. C. Rudolph pers. obs.). Cavity trees and adjacent trees also have loose bark persistently scaled from their boles by Red-cockaded Woodpeckers (Jackson 1978b, Ligon 1970). This behavior results in a reduction of the surface roughness of these trees. Several functions of resin well excavation and bark scaling have been suggested. Lay and Russell (1970) hypothesized a social context for these behaviors, resulting in communication of colony location and/ or active status. The majority of hypotheses, however, have involved some aspect of cavity protection, either from predators or potential com-petitors. Pearson et al. (1942) suggested that resin flows were a "sticky and effective barrier against ants and flying squirrels." Steirly (1957) es-sentially agreed, and Dennis (1968) suggested defense against avian usur-pers. Ligon (1970), Dennis (1971a), and Jackson (1978a) hypothesized that protection from predatory snakes was the primary function.

In this paper we quantify the ability of rat snakes to climb Red-cockaded Woodpecker cavity trees, scaled trees, and control trees to evaluate the effectiveness of the resin barrier.

METHODS

Nine rat snakes (*E. o. lindheimeri*) ranging from 52–180 cm in total length were captured in Nacogdoches County, Texas. Snakes were housed in glass aquaria provided with soil substrate, water, and food. Climbing trials were conducted in active Red-cockaded Wood-pecker colonies located in Angelina County, Texas. The primary tree species used for cavity construction by Red-cockaded Woodpeckers in this area is longleaf pine (*Pinus palustris*), and all climbing trials used this species. Experimental trees were chosen based on the following criteria. Cavity trees (N = 3) were selected that exhibited a profuse coating of fresh resin that extended from the cavity to near ground level. Resin was present throughout

the 5-m course and was profuse for 4–4.5 m. Trees that had experienced extensive removal of loose bark by Red-cockaded Woodpeckers, hereafter termed scaled trees (N = 4), were chosen based on extent of bark removal (maximum) and similarity in size to cavity trees. Control trees (N = 4), unaltered by Red-cockaded Woodpecker activity, were chosen based on similarity in size to cavity and scaled trees. The diameters at breast height of all trees were within the range of 47–62 cm.

We established a 5-m climbing course on the trunk of each tree beginning at 1 m above ground level and extending to 6 m above ground level. The course was delineated by short strips of tape applied at 1-m intervals to the bark surfaces. In the case of cavity trees, the course was established on the side of the tree having the most active and copious resin accumulation. Snakes were tested for climbing ability when air temperatures were between 24 and 28°C. Use of molting and recently fed snakes was avoided. Snakes were placed on trunks with their heads positioned at the 1-m mark. The general response was for the snake to grip the bark surface and begin climbing. Most climbed continuously until their heads reached the level of the 6-m tape, when they were removed from the tree. Snakes that stopped climbing for extended periods (>5 sec) were gently prodded near their posterior end using a telescoping fishing pole. This resulted in continued climbing and avoided the influence of long pauses on climbing rates. Snakes that refused to initiate climbing at the 1-m mark, usually by falling or climbing toward the ground, were an occasional problem. Most performed well in subsequent trials. Number of trials per snake varied from 9–11.

Climbing trials were conducted over a period of 60 days after capture of the snakes. To avoid reduced performance due to previous exertion, trials of individual snakes were limited to a maximum of two per day and did not exceed one trial per hour. Trials on cavity trees were limited to one per day per snake to avoid the effects of accumulated resin. A minimum of five days separated trials using cavity trees. For each trial we recorded tree class (cavity, scaled, control), snake total length, and elapsed time of climb. Trials were terminated when snakes fell. In these instances partial distances and elapsed times were recorded.

RESULTS

Preliminary results indicated that climbing rates were influenced by tree diameter. Snakes experienced more difficulty climbing larger diameter trees, presumably due to smoother bark and a greater abundance of easily dislodged bark fragments. This source of variation was substantially reduced in the present study by using only relatively large trees (dbh's of 47–62 cm).

Sixty three trials were conducted on control and scaled trees. In 62 of these trials the snakes successfully completed the 5-m course. No significant difference in climbing success between control and scaled trees was found ($G = 0.52$, $P > 0.05$, df = 1, Yates' correction). In contrast, only three of 18 climbing attempts on cavity trees were successful. Snakes were less likely to climb cavity trees successfully than control and scaled trees combined ($G = 59.44$, $P < 0.001$, df = 1, Yates' correction). The three successful climbs were performed by the two smallest snakes in the sample of nine snakes.

Climbing rates were compared using a repeated measures ANOVA (Table 1). Rate of climbing was the dependent variable; tree class and
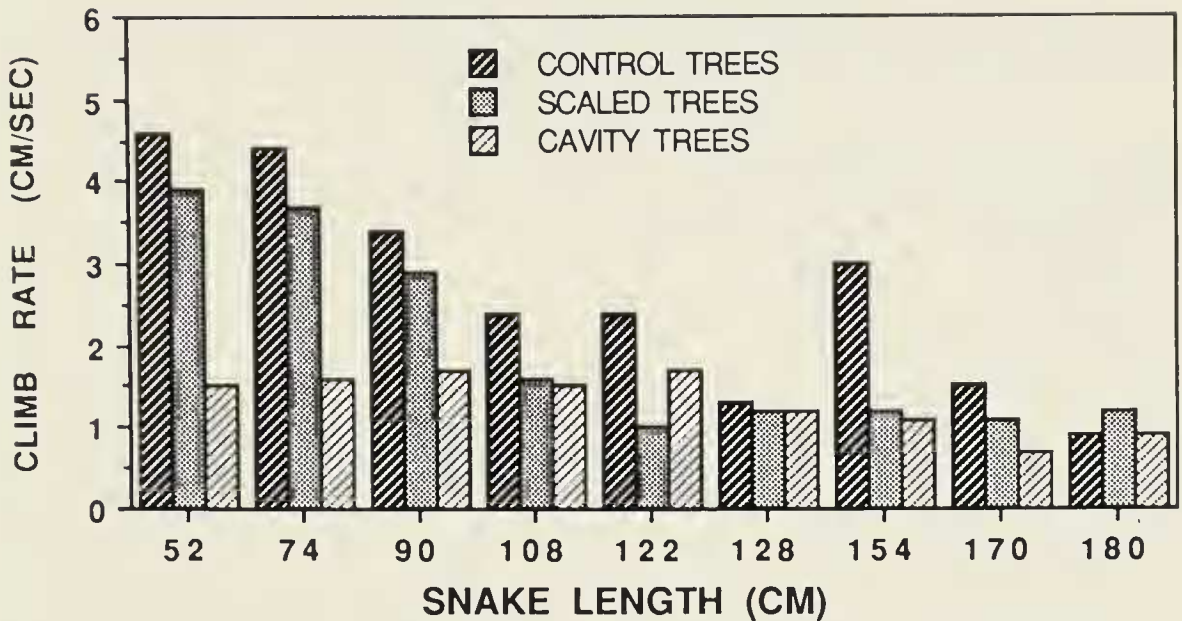
RAT SNAKE CLIMB RATES

FIG. 1. Climbing rates of rat snakes (*Elaphe obsoleta*) on control, scaled, and cavity trees.

snake total length were the two treatments. The results indicate a significant effect of both treatments (tree class and snake total length) on climbing rate ($P < 0.01$). Larger snakes required progressively more time to complete the experimental climbs, and this pattern was evident across all three tree classes (Fig. 1). The significant effect of tree class resulted from slower climbing rates for scaled trees and cavity trees compared to control trees. Compared to control trees, the smallest individuals experienced relatively little difficulty on scaled trees, but considerable difficulty on cavity trees (see Fig. 1). Larger individuals experienced substantial difficulty on both scaled and cavity trees.

Observation of snakes during the climbing trials provides additional information on several factors contributing to the pattern in climbing rates. Snake size related to climbing ability in two ways. First, the smaller snakes were generally able to insinuate their bodies into crevices between adjacent bark plates and effectively follow these anastomosing crevices up the trunk of the tree. Progressively larger snakes were less able to take advantage of this strategy and relied on a combination of crevices and protruding bark fragments to provide purchase points on the trunks. Searching for suitable paths up the trunk consumed progressively more time with increasing snake size. Second, the larger more massive snakes commonly dislodged loose bark fragments during climbing activity. Thus additional time was required to locate alternate purchase points as well

TABLE 1

ANALYSIS OF THE EFFECT OF TREE CLASS AND SNAKE TOTAL LENGTH ON CLIMBING RATE
USING A REPEATED MEASURES ANOVA

Source of variation	Sum of squares	df	Mean square	F
Mean	245.81	1	245.53	196.53**
Tree	16.09	2	8.05	6.43*
Snake	58.82	8	7.35	5.88*
Error	18.76	15	1.25	

** $P < 0.001$, * $P < 0.01$.

as often laborious recovery from near falls. These two factors appeared to be the primary contributors to the relationship between climbing rates and snake length.

Tree class had a pronounced effect on climbing behavior. Scaled trees, as compared to control trees, presented fewer purchase points for climbing snakes. As a result, snakes climbing scaled trees progressed with more difficulty and spent more time searching for a suitable route. Cavity trees also lacked rough bark, and in addition resin effectively smoothed over remaining irregularities, presenting the snakes with a relatively smooth surface. Initially snakes attempting to climb cavity trees progressed reasonably well, but as climbs continued the snakes experienced rapidly increasing difficulty. They were unable to maintain purchase points on the trunks over progressively increasing portions of their length, and most eventually fell. Even smaller individuals that successfully completed climbs experienced severe difficulties during the final portions of the climbs.

Examination of snakes immediately after climbing attempts on cavity trees revealed minimum amounts of resin adhering to their ventral surfaces. Small resin patches, a few mm in length, occasionally were noted. However, the overlapping surfaces of the ventral scales commonly had minute amounts of resin adhering to them, and these were often positioned such that they contacted adjacent scales. The result was a loss of mobility of the ventral scales important in this type of climbing.

Immediately after unsuccessful climbing trials on cavity trees, several snakes were observed on the ground. Their progress and behavior appeared normal. These individuals were also placed on control trees and their climbing efforts observed. They were unable to climb, or experienced considerable difficulty. Their behavior closely resembled that exhibited during climbs on resin-coated cavity trees. Residual resin reducing scale mobility was the probable cause of this climbing difficulty.

DISCUSSION

The rat snake is a common semiarboreal species found throughout the range of the Red-cockaded Woodpecker, with numerous recognized subspecies (Conant 1985).

The climbing abilities of *E. obsoleta* are well known (Curran and Kauffeld 1937, Wright and Wright 1957). Prey composition data indicate that birds and their eggs comprise a significant percentage of the diet of *E. obsoleta,* at least during avian breeding periods (Fitch 1963, Hensley and Smith 1986). Dennis (1971a) and Jackson (1978a) document four instances of *E. obsoleta* gaining access to Red-cockaded Woodpecker cavities. Two involved empty cavities, one cavity was occupied by flying squirrels (*Glaucomys volans*), and one cavity contained nestling Red-cockaded Woodpeckers. However rat snakes have difficulties in traversing the resin-coated surfaces (Dennis 1971a, Jackson 1978a, Summerour 1988). All observations of rat snakes successfully gaining access to cavities involve cavities whose resin barrier was compromised.

Jackson (1974) simulated resin-coated pine trunks in a laboratory setting and quantified rat snake climbing frequencies. A 2-cm band of fresh resin did not reduce climbing frequency; the snakes easily were able to arch their bodies over the resin band. The coating of extensive portions of the trunk with resin drastically reduced climbing frequencies compared to controls. Climbing frequency was also monitored during a subsequent 24-day period as the fresh resin dried. A significant increase in climbing frequency occurred with progressive drying of the resin.

In Jackson's (1974) experimental protocol, snakes that climbed resin-coated trunks experienced significant resin accumulation on their bodies. Abnormal behavior consisting of writhing and holding the body in stiff loops resulted. One individual subsequently died, possibly as a result of toxic effects of the resin. Jackson concluded that the snakes were affected by the stickiness of the resin, which cemented some of the scales together, and possibly by the potentially toxic effects of resin constituents, especially phenols.

The results presented support the hypothesis that resin wells and the resulting resin coating adjacent to Red-cockaded Woodpecker nest and roost cavities reduces access to these cavities by *E. obsoleta,* potentially the most significant snake predator of cavity-nesting birds in the southeast United States. The effectiveness of the resin barrier is indicated by the low incidence of climbing success (3/18 attempts) exhibited by snakes in the experiment. In an actual predation attempt, snakes would be required to negotiate the final distance to the cavity entrance, an additional 1–2 m in the case of the experimental trees, which the experimental climbing

course did not include. This area typically contains the heaviest and freshest resin accumulations. Consequently, cavity protection should be even more effective than these data indicate.

The scaling of loose bark from trees adjacent to cavity trees had no effect on rat snake climbing success. The reduced roughness of the trunk did, however, reduce the climbing rate of the snakes. Extensive scaling of loose bark from the cavity tree results in a smoother trunk and more even coverage by flowing resin. In this context the bark scaling behavior of Red-cockaded Woodpeckers undoubtedly increases the effectiveness of the resin barrier.

Jackson (1974) suggested that both the physical stickiness of the resin and potential toxic effects of resin deterred rat snakes. Jackson's experimental protocol resulted in copious amounts of resin adhering to the experimental snakes. In contrast, the protocol followed in our experiments, which closely resemble the actual situation faced by predatory snakes in the field, resulted in minimal amounts of resin accumulating on the ventral surfaces of the snakes. However, the mechanical effects of small amounts of resin picked up by the overlapping surfaces of individual scales, resulting in a tendency of adjacent scales to adhere, reduced the mobility of the ventral scales, and resulted in inability to climb. The limited direct contact with resin and the time involved in climbing reduces the probability of toxic effects of resin constituents. However, the potential repellent/toxic properties of resin constituents under natural conditions need to be tested further.

Elaphe obsoleta is an abundant and efficient predator on nesting birds in southeastern United States pine forests. Although data on actual predation rates are not available, anecdotal evidence suggests that it is a significant factor confronting many species of birds, including Red-cockaded Woodpeckers. Red-cockaded Woodpeckers exhibit an elaborate behavioral repertoire that produces a resin barrier effective in reducing access of rat snakes to their roost and nest cavities. J. R. Walters (in press) and J. A. Jackson (pers. comm.) indicate that Red-cockaded Woodpeckers have an extremely low nest predation rate compared to other cavity-nesting species. We support the hypothesis that reduction of snake predation, primarily by those in the genus *Elaphe,* is a major selective factor in the evolution of the behaviors of Red-cockaded Woodpeckers that result in the maintenance of resin coatings on cavity trees. Additional data quantifying actual snake predation rates on nesting birds in southeastern pine forests and the effectiveness of resin barriers in actually reducing snake predation would provide further insight.

The alternative hypotheses that have been proposed as selective factors culminating in the production of resin coating on Red-cockaded Wood-

pecker cavity trees are not mutually exclusive. Hypotheses proposed concern three general types of selective benefits; communication functions (Lay and Russell 1970), reduction of non-snake predation (Pearson et al. 1942, Ligon 1970, Dennis 1971a), and reduction of competition for cavities by other species (Ligon 1970, Dennis 1971b). Specific evaluation of these alternative hypotheses is necessary to determine if they are significant factors in the evolution of Red-cockaded Woodpecker behavior related to resin well construction on cavity trees.

ACKNOWLEDGMENTS

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